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Effect of Sucrose Concentration on Carbohydrate Metabolism in *Bemisia argentifolii*: Biochemical Mechanism and Physiological Role for Trehalulose Synthesis in the Silverleaf Whitefly

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Uptake and metabolism of sucrose by adult silverleaf whiteflies (*Bemisia argentifolii*) were investigated on defined diets containing sucrose concentrations from 3 to 30% (w/v). At an optimal pH of 7, the volume of liquid ingested decreased with increasing dietary sucrose concentration, but the amount of sucrose ingested showed a net increase. Above a dietary sucrose concentration of about 10%, a greater amount of the ingested carbon was excreted by the whiteflies than was retained, and the proportion that was excreted increased progressively with increasing dietary sucrose concentration. Carbohydrate analysis showed that the composition of excreted honeydew changed from predominantly glucose and fructose at low dietary sucrose concentrations to predominantly trehalulose at high concentrations, with little change in the proportion of larger oligosaccharides. Measurements of whitefly trehalulose synthase and sucrase activities revealed that the enzymatic potential for metabolizing sucrose shifted from favoring sucrose hydrolysis at low sucrose concentrations to sucrose isomerization at high sucrose concentrations. Thus, the amount of trehalulose synthesized by the silverleaf whitefly was directly related to the properties of trehalulose synthase and sucrase and the concentration of sucrose in the diet. We propose that trehalulose is synthesized for excretion when the carbon input from sucrose is in excess of metabolic needs. Published by Elsevier Science Ltd

Bemisia argentifolii Whitefly Carbohydrate metabolism Trehalulose

INTRODUCTION

The silverleaf whitefly, *Bemisia argentifolii* Perring and Bellows (Homoptera: Aleyrodidae), is a serious pest world-wide (Byrne and Bellows, 1991; De Barro, 1995). The insect is a vector for numerous infectious plant viruses that damage a variety of crop species (Cock, 1993; Brown, 1994). Whiteflies can attain almost plague-like populations on cotton, causing severe reductions in yield (Gerling *et al.*, 1980; Bellows and Arakawa, 1988; Henneberry *et al.*, 1995). In addition, fiber from whitefly-infested cotton becomes 'sticky' from deposits of honeydew on the lint (Henneberry *et al.*, 1995). 'Stickiness' reduces the market value of the crop because sticky lint is difficult or impossible to gin and process at textile mills, and is often discolored from microbial flora that grow on the honeydew sugars.

The nutritional requirements of phloem-feeding insects have been examined extensively, but the vast majority of these studies have focused on aphids (c.f. Auclair, 1963; Walters and Mullin, 1988; Mittler and Meikle, 1991; Simpson *et al.*, 1995; Rhodes *et al.*, 1996). Although whiteflies, like aphids, are homopterans, whiteflies possess Malpighian tubules and a well-developed filter chamber (Goodchild, 1966; Cicero *et al.*, 1995), structures that are not present in most aphid species (Auclair, 1963 and references therein). Because of these anatom-

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ical differences, the nutritional biochemisty of whiteflies and aphids may differ substantially.

An aspect of *Bemisia* carbohydrate metabolism that is unique among whiteflies (Hendrix *et al.*, 1992), and that has not been reported in other insects is the synthesis of the sugar trehalulose (Bates *et al.*, 1990; Byrne and Miller, 1990). Trehalulose is a disaccharide that often occurs as a major component of *Bemisia* honeydew (Byrne and Miller, 1990; Tarcznski *et al.*, 1992; Hendrix and Wei, 1994). Trehalulose is formed by rearrangement of the glycosidic bond of sucrose from the two to the one position of fructose, i.e. α-D-glucose (1,2) β-D-fructose→α-D-glucose (1,1) D-fructose. The enzyme that catalyzes this isomerization, trehalulose synthase, has been identified and described in several bacterial species (Cheetham, 1984; Park *et al.*, 1992). Trehalulose synthase also occurs in *B. argentifolii* (Davidson *et al.*, 1994), but the *Bemisia* enzyme has not been characterized.

In the present study, we examine the effect of dietary sucrose concentration on the uptake and metabolism of sucrose by the silverleaf whitefly. The results show that metabolism of sucrose by *B. argentifolii* is remarkably consistent with the kinetic parameters of the enzymes that isomerize and hydrolyze sucrose, and suggest a possible physiological role for trehalulose.

MATERIALS AND METHODS

Chemicals

Inulin-[^{14}C]-carboxylate (9 mCi mmol^{-1}), [U-^{14}C]sucrose (677 mCi mmol^{-1}) and [^{35}S]methionine/cysteine (75:15, 1000 Ci mmol^{-1}) were purchased from Amersham Life Science (Arlington Heights, IL). Unless indicated otherwise, all other reagents were from Sigma Chemical Co. (St Louis, MO)

Plant and insect material

Silverleaf whiteflies were reared on cotton plants (*Gossypium hirsutum* L., var. Coker 100A glandless). Plants were grown in screened boxes within a glasshouse under a 12 h day/night temperature regime of 35/25°C and natural photoperiod.

Feeding experiments

Micro spin-filtration devices (Lida Manufacturing Co., Kenosha, WI) were adapted for use as feeding devices by removing the 0.45 μ filter and plastic supporting screen from the filtration apparatus. The open bottom was sealed with a layer of stretched parafilm and feeding solution was added to the cylinder. The modified micro spin-filtration units provided a 0.2 cm^2 surface for feeding. To prevent evaporation, the top of the filtration device was loosely covered with the yellow cap that was supplied with the micro spin-filtration apparatus. To prevent whiteflies from leaving the feeder, the feeder units were inserted into 2 ml microfuge tubes that had been shortened to a length of 1.5 cm. These tubes also served as collectors for the honeydew that was produced during the feeding experiments.

Except where indicated, feeding solutions contained 0.1 M potassium phosphate, pH 7, the indicated concentrations of sucrose, 1–14 μCi of radioactive tracer in the form of inulin-[^{14}C]-carboxylate, [^{35}S]Met/Cys or [U-^{14}C]sucrose, and 1 μl of yellow food coloring (DecACake, Burns Phillips Food Inc., San Francisco, CA) in a total volume of 100 μl. Adult silverleaf whiteflies were freshly collected by aspiration, immobilized by chilling for 5 min at 4°C, and then transferred to the wells of a solid polypropylene microfuge rack (approximately 50 insects well^{-1}). Feeding devices were inserted into the insect-containing wells in the light at 24°C to initiate feeding. After 1 h, approximately 25 whiteflies were attached to the parafilm bottom of each feeding device and appeared to be actively feeding. At this time, the feeding devices were carefully removed from the microfuge rack and inserted into collection tubes. After 4 h in the light at 24°C, the feeding devices with collection tubes attached were chilled to 4°C to immobilize the whiteflies. Whiteflies were collected from the parafilm and collection tube, and the honeydew was recovered by rinsing the collection tube with water. Radioactivity was determined by liquid scintillation spectroscopy using a Packard 2200CA liquid scintillation counter (Packard Instrument Company, Downers Grove, IL) after dissolving the whiteflies and honeydew from each of the feeders in BioSafe II liquid scintillation fluid (Research Products International Corp., Mount Prospect, IL). Four to eight separate feeders were used for each treatment. The results presented are the means plus standard error of the feeders, each containing 25 whiteflies.

Carbohydrate analysis

The carbohydrate composition of the honeydew was determined by high-performance liquid chromatography (HPLC) as described previously (Hendrix and Wei, 1994). The pooled contents of four collection tubes representing each treatment were lyophilized in a Speed-Vac concentrator. Dried material was resuspended in 50 μl H_2O and 25 μl was chromatographed using HPLC.

Enzyme assays

Approximately 100 freshly collected adult whiteflies were homogenized at 4°C in a Ten Broeck glass homogenizer containing 1 ml of 100 mM 3-(N-morpholino)-2-hydroxypropane-sulfonic acid (MOPS)-KOH, pH 7, 5 mM $MgCl_2$, 1% (v/v) Triton X-100 and 5 mM 2-mercaptoethanol. The homogenate was centrifuged at 20 000×***g*** for 10 min and the supernatant used for the assays.

Trehalulose synthase activity was measured by incubating an aliquot of the supernatant at 30°C in a 50 μl assay containing 100 mM MOPS-KOH, pH 7, 5 mM dithiothreitol and the indicated concentrations of sucrose. Reactions were terminated after 30 min by boiling for

2 min and then centrifuged for 3 min at 13 000×*g* to remove denatured protein. The amount of trehalulose produced in the assay was determined by HPLC analysis of the supernatant (Hendrix and Wei, 1994). Trehalulose was not detected in zero time controls in which the supernatant was boiled for 2 min prior to assay.

Sucrase activity was determined spectrophotometrically at 30°C by linking sucrose hydrolysis to $NADP^+$reduction via hexokinase and glucose-6-phosphate dehydrogenase. An aliquot of the whitefly supernatant was added to 0.5 ml assays containing 100 mM MOPS, pH 7.0, 5 mM 2-mercaptoethanol, 5 mM $MgCl_2$, 2 mM ATP, 2 mM $NADP^+$, 2 IU hexokinase, 1 IU glucose-6-phosphate dehydrogenase and the indicated concentrations of sucrose. Sucrose hydrolysis was determined continuously by monitoring the sucrose-dependent increase in A_{340} caused by the reduction of $NADP^+$. Control experiments showed that whitefly extracts contained sufficient phosphoglucoisomerase activity to convert Fru-6-P to Glu-6-P as rapidly as it was produced. Thus, the rate of NADPH formation was twice the rate of sucrose hydrolysis. Apparent K_M and V_{max} values of both trehalulose synthase and sucrase were determined by nonlinear regression analysis of duplicate assays using the GraFit program (Leatherbarrow, 1992). A unit of activity (U) is equal to 1 μmol of sucrose hydrolyzed or isomerized per min.

Substrate specificity of sucrase

To determine the relative rates of hydrolysis of trehalulose, sucrose and stachyose, sucrase was partially purified from whitefly extracts by precipitation with ammonium sulfate (35–60%) and polyethylene glycol (25%). Trehalulose was produced by incubating crude whitefly extracts overnight at 30°C with 0.7 M sucrose. Trehalulose and sucrose in the reaction mixtures were separated by HPLC on a 4.6×250 mm Absorbosil-NH_2 column (Alltech Inc, Deerfield, IL) using an isocratic mobile phase of acetonitrile: H_2O (77.5:22.5). Fractions containing sucrose and trehalulose were lyophilized and the dried material was resuspended in a small amount of H_2O. The isolated sucrose and trehalulose, as well as commercially prepared stachyose, were incubated with partially purified sucrase at 30°C for 15 min in an assay containing 0.1 M MOPS, pH 7, 5 mM 2-mercaptoethanol. Reactions were terminated by boiling. The rates of hydrolysis of the three substrates were determined from the amount of product formed and substrate used after separation and quantitation by HPLC (Hendrix and Wei, 1994).

Miscellaneous

Protein concentration in whitefly extracts was determined by the method of Bradford (1976) using bovine serum albumin as the standard.

RESULTS

Characterization of the feeding system

A simple, small volume system was developed for feeding silverleaf whiteflies on a defined diet. The feeder was ideal for use with radioisotopic tracers or expensive chemicals, since the entire feeding surface could be completely covered with as little as 50 μl of solution. In addition, feeding solution could be adjusted or removed from the cylindrical filtration device without disturbing feeding. Addition of trace amounts of radiolabeled material to the defined diets provided a means for determining the total volume of solution ingested. Preliminary results showed that the calculated rates of dietary uptake were similar when based on the amount of either [^{35}S]Met/Cys or inulin-[^{14}C]-carboxylate taken up (data not shown). With [^{35}S]Met/Cys, about 52% of the radiolabel was retained in the whitefly body after 4 h of feeding, while the remainder was excreted in the honeydew. In contrast, greater than 90% of the ingested inulin-[^{14}C]-carboxylate was recovered in the honeydew as expected for a compound that cannot be metabolized by insects (Fischer *et al.*, 1984; Simpson *et al.*, 1995).

The optimum pH for ingestion from a diet containing 20% sucrose was between 6.5 and 7.5 (Fig. 1). We therefore chose a pH of 7 for all subsequent experiments. Visual observations showed that whiteflies actively fed for 24–48 h on a sucrose diet buffered at this pH, and had a mortality rate of less than 20% during this period.

Effect of sucrose concentration on its uptake and metabolism

The total volume of solution ingested by the whiteflies decreased progressively as the sucrose concentration increased from 3 to 30% (Fig. 2). However, the higher sucrose concentration offset the decrease in volume so that the amount of sucrose ingested increased with dietary sucrose concentration.

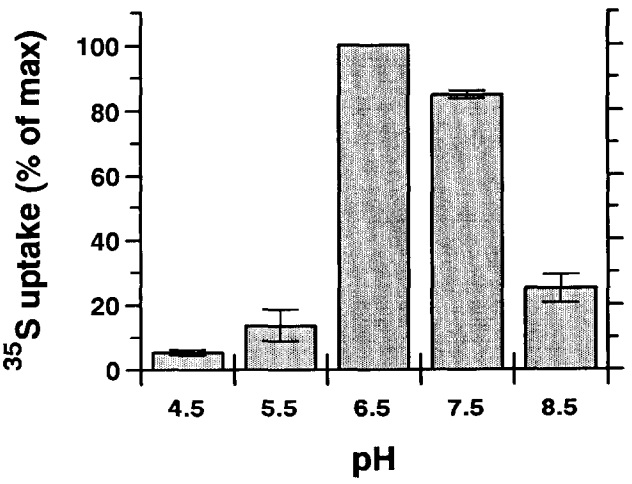

FIGURE 1. Effect of pH on uptake of diet solution by silverleaf whiteflies. Whiteflies were fed on solutions containing 20% sucrose, 0.14 μM [^{35}S]Met/Cys (14 μCi) and 100 mM potassium phosphate at the indicated pH.

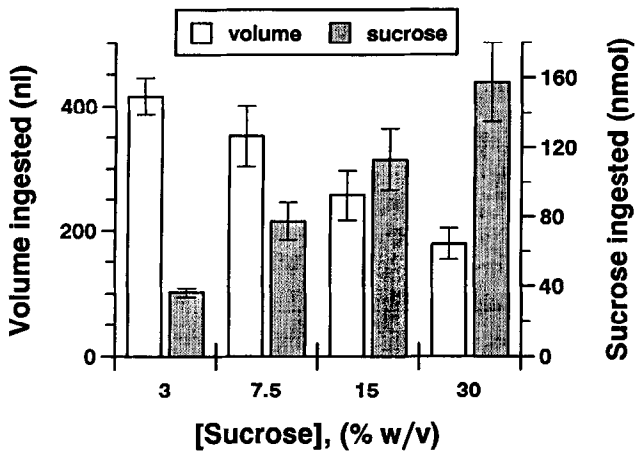

FIGURE 2. Effect of sucrose concentration on uptake of solution by silverleaf whiteflies. Whiteflies were fed on solutions containing 100 mM potassium phosphate, pH 7, 1 μCi inulin-[^{14}C]-carboxylate and sucrose at the indicated concentrations. The volume of solution (open bar) and the amount of sucrose (closed bar) ingested were determined from the amount of radioactivity ingested.

To determine the effect of dietary sucrose concentration on carbon partitioning and metabolism, silverleaf whiteflies were fed on diets containing various concentrations of radiolabeled sucrose. The amount of radiolabeled carbon excreted in the honeydew increased markedly with increasing concentrations of sucrose in the diet, exhibiting a progressively greater increase with concentration over the entire range of dietary sucrose concentrations (Fig. 3). The amount of radiolabeled carbon retained in the whitefly body also increased, but the increase was much more gradual above a dietary sucrose concentration of 7.5%. For example, over the range of dietary sucrose concentrations from 7.5 to 30%, the amount of carbon that partitioned into the body increased only two-fold, whereas the amount that was excreted in the honeydew increased five-fold. At sucrose concentrations of 3 and 7.5%, there was slightly more radioactivity in the whitefly body compared with the honeydew. In contrast, at 30% sucrose more than twice as much carbon was excreted in the honeydew than was retained in the whitefly body.

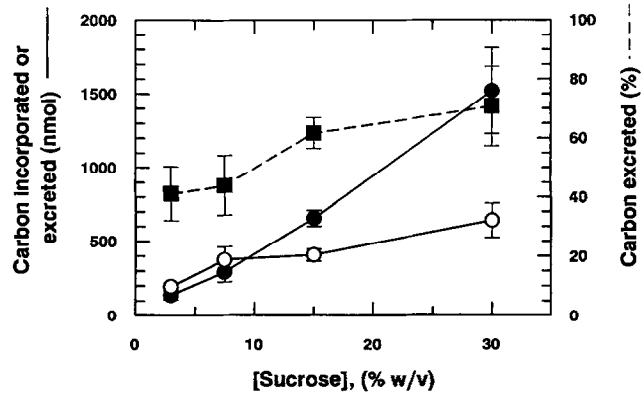

FIGURE 3. Effect of sucrose concentration on the excretion and incorporation of carbon by silverleaf whiteflies. Whiteflies were fed on solutions containing 100 mM potassium phosphate, pH 7, 14 μCi [U-^{14}C]sucrose and unlabeled sucrose at the indicated concentrations. The amount of carbon excreted (●) was determined by measuring the amount of radioactivity in the honeydew. The amount of carbon incorporated (○) was determined by measuring the amount of radioactivity retained in the whitefly. The dashed line indicates the percentage of carbon excreted (■).

The composition of the excreted carbohydrates showed that the level of dietary sucrose had an effect on the metabolic fate of ingested sucrose. Representative chromatograms at a high (30%) and low (5%) sucrose concentration are presented in Fig. 4. In general, whiteflies feeding on solutions containing less than 10% sucrose produced honeydew that consisted of primarily glucose and fructose with little trehalulose. In fact, in some experiments trehalulose was virtually undetectable in the honeydew when dietary sucrose concentration was at or below 5% (data not shown). As dietary sucrose concentration increased, trehalulose became the predominant carbohydrate of honeydew.

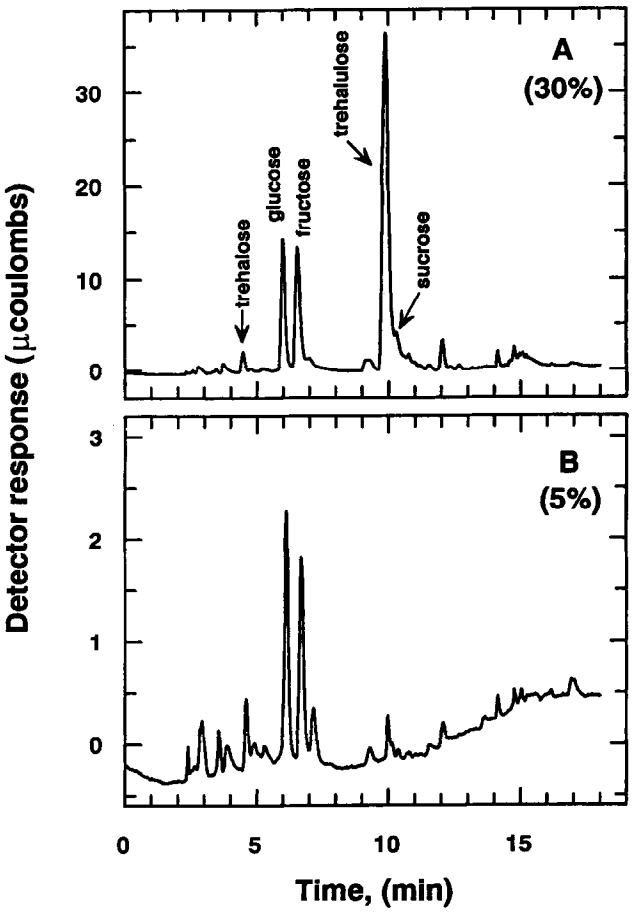

FIGURE 4. Comparison of the components of whitefly honeydew after feeding on solutions containing 5 and 30% sucrose. Whiteflies were fed on solutions containing 100 mM potassium phosphate, pH 7, 0.14 μM [^{35}S]Met/Cys (14 μCi) and either 30% (A) or 5% (B) sucrose, after which the individual components of the honeydew were separated by HPLC and detected using a pulsed amperometric detector. The figure shows the chromatograms of the HPLC separation. Detector sensitivity toward trehalulose is 57% of that of glucose and fructose. Volumes ingested on 5 and 30% sucrose were 473±35 and 274±42 nl, respectively.

To quantitate the above results, honeydew from whiteflies feeding on various concentrations of radiolabeled sucrose was separated and analyzed. The absolute amounts of all the honeydew carbohydrates increased with increasing sucrose concentration [Fig. 5(A)], but the increase was much more marked for trehalulose and carbohydrates with a degree of polymerization (dp) ≥3 (i.e. dp3) than for sucrose and the monosaccharides. Consequently, the composition of the carbohydrates in the honeydew changed from predominantly glucose and fructose and ≥dp3 oligosaccharides at low dietary sucrose concentrations to predominately trehalulose and ≥dp3 oligosaccharides at high concentrations [Fig. 5(B)]. Interestingly, the proportion of sucrose converted to ≥dp3 oligosaccharides was similar at the various sucrose concentrations, and there was no change in the relative distribution among the various ≥dp3 oligosaccharides (data not shown).

Enzymatic hydrolysis and isomerization of sucrose

The potential for conversion of sucrose to trehalulose or hydrolysis to glucose and fructose was investigated by conducting enzyme assays with whole body extracts of adult whiteflies. Preliminary experiments showed that whitefly extracts catalyzed trehalulose synthesis and also contained a separate enzymatic activity that hydrolyzed sucrose to glucose and fructose. Partially purified preparations containing only the sucrolytic activity were also capable of hydrolyzing *p*-nitrophenol-glucose, but not stachyose [α-D-galactose (1,6) α-D-galactose (1,6) α-D-glucose (1,2) β-D-fructose]. Since invertases (i.e. β-fructofuranosidases) readily hydrolyze stachyose, these results indicate that most if not all of the sucrose hydrolytic activity was associated with a sucrase, an α-glucopyranosidase. Partially purified whitefly sucrase was able to hydrolyze trehalulose; however, at equivalent concentrations the rates of trehalulose hydrolysis were only about 10% of the rate of sucrose hydrolysis (data not shown).

The effect of sucrose concentration on the activities of trehalulose synthase and sucrase are presented in Fig. 6. Sucrase activity was saturated by sucrose concentrations greater than 100 mM, whereas trehalulose synthase activity required much higher levels of sucrose for saturation. The apparent K_M values for the sucrase and trehalulose synthase were 15±2 and 181±8 mM, respectively, equivalent to 0.5 and 6.2% (w/v). The maximum velocity of trehalulose synthase, 1.3 U mg protein^{-1}, was 2.5-fold higher than for sucrase. However, because of the large difference in sucrose affinity between the two enzymes, the rate of sucrose hydrolysis by sucrase at low concentrations of sucrose was significantly higher than the rate of sucrose isomerization via trehalulose synthase (Fig. 6, inset).

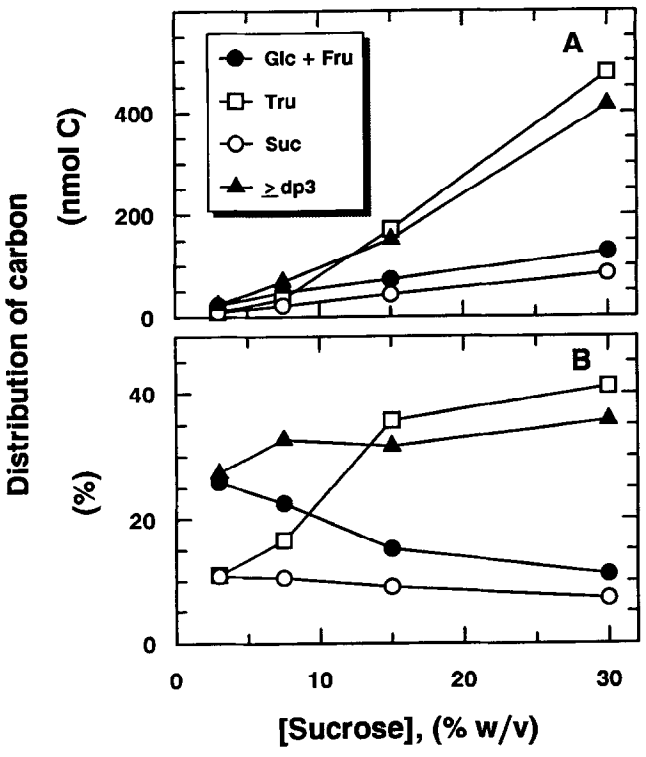

FIGURE 5. Effect of sucrose concentration on the distribution of newly acquired carbon among the various components of whitefly honeydew. Whiteflies were fed on solutions containing 100 mM potassium phosphate, pH 7, 14 μCi [U-^{14}C]sucrose and unlabeled sucrose at the indicated concentrations. The distribution of carbon among glucose and fructose (●), trehalulose (□), sucrose (○) and ≥dp3 sugars (▲) was determined by measuring the radioactivity of the individual components after separation by HPLC. (A) The amount of carbon in the various components; (B) The per cent distribution.

DISCUSSION

Uptake and metabolism of sucrose by the silverleaf whitefly

The inclusion of radiolabeled tracer enabled accurate measurement of the volume of feeding solution ingested and excreted by silverleaf whiteflies on defined diets. The maximum volume ingested over a 4 h feeding experiment

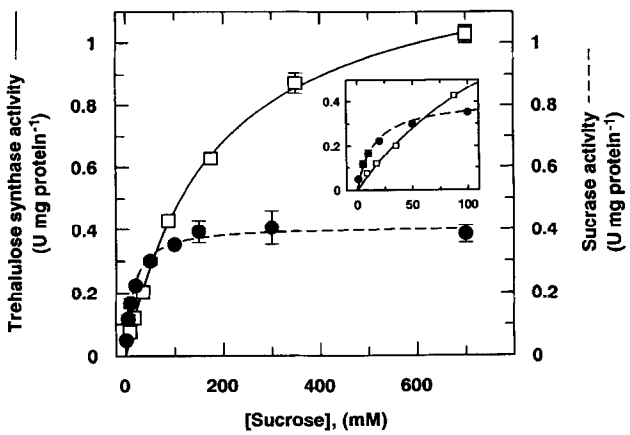

FIGURE 6. Effect of sucrose concentration on the activities of trehalulose synthase (□) and sucrase (●) in extracts of the silverleaf whitefly. The inset shows the activities at low substrate concentrations. Error bars represent standard errors.

was 600 nl per feeder, which is equivalent to an average feeding rate per whitefly of about 6 nl h^{-1}. The pH of the diet markedly affected the rate of solution ingestion. Rates were highest at pH values of 6.5 and 7.5, and considerably lower above and below these pH values. A similar effect of pH was reported by Berlinger *et al.* (1983), who showed that the number of resting whiteflies and the per cent survival on buffered sucrose solutions were highest at neutral pH values.

The concentration of sucrose in the diet also affected the volume of solution ingested by the whiteflies. The volume ingested was greatest at the lowest sucrose concentration and decreased with increasing concentrations of dietary sucrose. Abisgold *et al.* (1994) and Simpson *et al.* (1995) obtained a similar result with the pea aphid, *Acyrthosiphon pisum*, and concluded that aphids regulate carbohydrate uptake primarily by altering consumption. The similarity of our results to their findings suggests that this conclusion is also applicable to whiteflies. The presence of amino acids in the diet is also known to affect the consumption of carbohydrates by aphids (Mitler, 1967; Abisgold *et al.*, 1994; Simpson *et al.*, 1995). The effect of amino acids on carbohydrate uptake by whiteflies is unknown since physiologically significant levels of amino acids were not included in the whitefly diets.

In a study of two aphid species, Mittler and Meikle (1991) showed that the volume of honeydew excreted by *Acyrthosiphon pisum* and *Myzus persicae* progressively decreased as the dietary sucrose concentration increased from 10 to 30%. We measured a similar response in whiteflies using the undigestable compound inulin-[^{14}C]-carboxylate. In the same study, the proportion of sucrose retained by *A. pisum* and *M. persicae* decreased as the dietary sucrose concentration increased from 10 to 40%. We observed a similar trend with whiteflies (Fig. 3). However, in comparison to aphids (see also Rhodes *et al.*, 1996), whiteflies excreted a much larger proportion of the ingested carbon.

Above a dietary sucrose concentration of about 10%, silverleaf whiteflies excreted a greater amount of carbon than they retained and the proportion of carbon that was excreted increased with increasing concentrations of sucrose in the diet. As in aphids, the increased partitioning of carbon to excretion was accompanied by a major change in the composition of the honeydew, including an increase in the absolute amount of ≥dp3 oligosaccharides. However, unlike in aphids (Fischer *et al.*, 1984; Walters and Mullin, 1988) the change in whitefly honeydew composition did not involve a change in the proportion of carbon partitioned into ≥dp3 oligosaccharides or in the composition of the ≥dp3 oligosaccharides. Instead, the major change in whitefly honeydew involved an increase in the proportion of trehalulose to hexose monosaccharides (i.e. glucose and fructose). Since plant species differ in their phloem sucrose concentrations (compare the work of Haritatos *et al.*, 1996 with Fischer and Gifford, 1986), the marked effect of sucrose concentration on trehalulose synthesis may account for some of the differences in whitefly honeydew composition on different plant hosts (Byrne and Miller, 1990; Hendrix *et al.*, 1992).

Some of the ingested sucrose was undoubtedly used by the whiteflies for respiration, but the amount was not measured. In locusts, respiration serves as a removal mechanism for excess carbohydrates (Zanotto *et al.*, 1993), and the same may apply for whiteflies. In an interesting study of the pea aphid, Rhodes *et al.* (1996) showed that respiration rates were similar at dietary sucrose concentrations of 11 and 22%, but decreased when the sucrose concentration in the artificial diet was changed from 22 to 0%. Measurements of respiration rates at various dietary sucrose concentrations are needed to determine if whiteflies consume excess carbohydrates by increasing respiration.

Biochemical mechanism for trehalulose synthesis at high dietary sucrose concentrations

The changes in honeydew sugar composition that occurred in response to a change in dietary sucrose concentration were entirely consistent with the kinetics and activities of the major whitefly enzymes responsible for isomerizing and hydrolyzing sucrose. Enzyme assays showed that trehalulose synthase from silverleaf whiteflies had a much higher maximum velocity than sucrase, but its affinity for sucrose was more than an order of magnitude lower. Thus, when these two enzymes act together on sucrose the enzymatic potential shifts with sucrose concentration from favoring sucrose hydrolysis and the resultant production of glucose and fructose at low sucrose concentrations, to sucrose isomerization and the production of trehalulose at high sucrose concentrations. Our measurements of the honeydew composition of whiteflies on various sucrose concentrations followed this pattern, indicating that sucrose metabolism in the whitefly reflects the kinetic parameters of trehalulose synthase and sucrase.

Possible physiological role for trehalulose synthesis

The effect of dietary sucrose concentration on carbohydrate metabolism in *B. argentifolii* suggests a possible physiological role for trehalulose. At low sucrose concentrations, a relatively large percentage of the newly ingested carbon was retained in the whitefly body presumably to satisfy nutritional requirements. At the same time, trehalulose constituted a much lower percentage of the total carbon in the honeydew than glucose and fructose. As the dietary sucrose concentration increased, a greater proportion of the ingested carbon was excreted and trehalulose became the most abundant component in the honeydew. That trehalulose was most abundant in silverleaf whitefly honeydew when the ingested sucrose was in excess of the insect's metabolic requirements indicates that trehalulose is primarily synthesized for excretion of excess carbon.

Synthesis of trehalulose from sucrose involves

rearranging the glycosidic bond of sucrose from the two to the one position of fructose. This rearrangement affords no advantage in terms of osmotic strength, but does significantly change the susceptability of the disaccharide molecule to hydrolysis by sucrase. Our data show that at equivalent concentrations silverleaf whitefly sucrase hydrolyzed trehalulose at only about 10% of the rate of sucrose hydrolysis. Because of the slower rate of hydrolysis, conversion of sucrose to trehalulose would tend to maintain ingested carbohydrate in the form of a disaccharide. Preserving carbon in the form of a dissacharide rather than two monosaccharides has obvious advantages in terms of osmotic potential. It is also possible that the reduced rate of disaccharide hydrolysis is required for metabolic homeostasis, ensuring that the levels of monosaccharides do not greatly exceed the metabolic needs of the insect. Both possibilities are consistent with an essential role for trehalulose synthesis in maintaining proper metabolic activity on a high sucrose diet. Thus, inhibiting trehalulose synthase may provide a strategy for controlling silverleaf whitefly on plant species such as cotton that translocate sucrose.

Unlike whiteflies, aphids respond to increasing dietary sucrose concentration by increasing the average size of their honeydew oligosaccharides (Fischer *et al.*, 1984; Walters and Mullin, 1988). The reason silverleaf whiteflies do not respond similarly is unknown, but may be related to the presence of a filter chamber. It is likely that this organ regulates the distribution of carbon between excreted and incorporated forms. Our data show that this regulation could easily be accomplished if the filter chamber housed the relevent enzymes for sucrose hydrolysis and isomerization. Alternatively, there is evidence to suggest that trehalulose synthase is associated with the endosymbiotic bacteria that reside in the well-developed mycetomes of the whitefly (Davidson *et al.*, 1994). Studies are in progress to further characterize sucrase and trehalulose synthase and to identify their locations within the whitefly body.

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